In situ variation in leaf anatomy and morphology of *Andira legalis* (Leguminosae) in two neighbouring but contrasting light environments in a Brazilian sandy coastal plain

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RESUMO – (Variação *in situ* em anatomia e morfologia foliar de *Andira legalis* (Leguminosae) em dois ambientes adjacentes, porém contrastantes quanto ao regime de luz, em restinga brasileira). *Andira legalis* (Vell.) Toledo é uma leguminosa arbustiva distribuída ao longo de planícies arenosas da costa brasileira. Tem ocorrência em ambientes florestais, sombreadas, ou em ilhas de vegetação de restingas abertas, onde é exposta à plena radiação solar. Estudos prévios relataram uma grande amplitude de variação morfo-fisiológica para esta espécie ao longo de um gradiente geográfico. Este estudo comparou morfologia e anatomia foliar de *A. legalis* em dois ambientes adjacentes porém contrastantes quanto ao regime de luz: uma floresta densa (sombreada) e uma formação arbustiva de Palmae (exposta à luz). Estudamos a amplitude de variação morfo-anatômica no interior de uma diminuta dimensão geográfica (0,5 ha). Parâmetros de anatomia foliar foram medidos para cinco folhas coletadas a partir de cinco plantas em cada habitat. Os parâmetros avaliados foram: espessura foliar e do mesofilo, espessura da parede celular periclinal externa, espessura adaxial e abaxial da epiderme, área da seção transversal do feixe vascular, e densidade de células epidérmicas comuns, estômatos e tricomas. Dados de morfologia foliar foram obtidos a partir de cinco folhas de cada uma de 20 plantas em cada sítio. Medidas de peso seco e fresco foram tomadas para a obtenção dos valores de massa específica foliar e suculência. Conforme era esperado, os valores de todos os parâmetros anatômicos e morfológicos, exceto densidade de tricomas, foram significativamente mais altos para as plantas expostas ao sol. Menos esperado, entretanto, foi a clara diferença qualitativa entre folhas de plantas expostas vs. sombreadas: nas expostas, o mesofilo apresentou simetria unilateral (*i.e.*, todo o mesofilo era ocupado por tecido fotossintético), enquanto nas sombreadas a simetria foi dorsiventral (*i.e.*, em parte parênquima paliçádico, em parte parênquima esponjoso). Tal amplitude de variação mostra que, mesmo em uma pequena área geográfica, *A. legalis* tem uma ampla plasticidade ecológica.

Palavras-chave: anatomia foliar, *Andira legalis*, floresta atlântica, plantas de sol e sombra, restinga

ABSTRACT – (*In situ* variation in leaf anatomy and morphology of *Andira legalis* (Leguminosae) in two neighbouring but contrasting light environments in a Brazilian sandy coastal plain). *Andira legalis* (Vell.) Toledo is a legume shrub widespread along the sandy plains of the Brazilian coast. It occurs both shaded, in forest habitats, or exposed to full sunlight, in the vegetation islands growing on sand deposits. Previous studies reported a high range of morpho-physiological variation for this species along a geographical gradient. This study compared leaf morphology and anatomy of *A. legalis* in two distinct but adjacent light environments: a dense forest (shaded) and a scrub of Palmae (exposed). We studied the amplitude of variation for these traits within a small (0.5 ha) geographical area. Leaf anatomy parameters were measured for five leaves collected from five plants in each habitat. The parameters measured were leaf and mesophyll thickness, thickness of the outer periclinal cell wall, thickness of the adaxial and abaxial epidermis and vascular bundle transversal section area, and also common epidermal cells, stomata and trichome density. Leaf morphology parameters were obtained from five leaves of each of 20 plants in each site. Dry and fresh weights were measured to obtain leaf specific mass and succulence. All anatomy and morphology parameters, except trichome density, were significantly higher for the sun-exposed plants. Less expected, however, was the marked qualitative difference between exposed and shaded plants: in the former the mesophyll had a unilateral symmetry (*i.e.*, the whole mesophyll occupied by photosynthetic tissue), whereas in the latter there was a dorsiventral symmetry (*i.e.*, partly palisade and partly spongy parenchyma). Such amplitude of variation shows that even within a small geographic area *A. legalis* has a broad ecological plasticity.

Key words: *Andira legalis*, Atlantic forest, leaf anatomy, restinga, sun-shade plants

Introduction

The Brazilian Atlantic forest complex is formed by different vegetation physiognomies (Rizzini 1979). In the montane forest, at the core of the complex, lies the highest species diversity and endemism. In contrast, the plant communities at the periphery of this forest are less structurally complex and are often less species diverse

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(Scarano 2002). One of these marginal habitats, called locally *restinga*, covers the sandy coastal plains of Brazil. This ecosystem is a mosaic of habitats, ranging from reptant beach vegetation to swamps, which collectively subject plants to more extreme environment conditions than the mesic montane forest, such as salinity, flooding, drought or heat (Lacerda *et al*. 1993). However, most plant species inhabiting the restingas originated in the montane forest (Rizzini 1979; Scarano 2002) and, thus, had the capacity to adjust and colonize this more severe environment. This ability might be the result of ecological advantage obtained by morpho-anatomical (Rôças *et al*. 2001) and physiological (Scarano *et al*. 2001; 2005; Duarte *et al*. 2005) modifications.

In restingas, although different communities frequently lie adjacent to each other (Lacerda *et al*. 1993), very few plants occur in more than one or two habitats. *Andira legalis* (Vell.) Toledo (Leguminosae-Papilionoidae) is one such plant. In the case studied here, light levels change abruptly between a forest and an adjacent open shrubland. In this ecotone, there is no transitional vegetation between these two contrasting formations (Cirne & Scarano 2001). Sun and shade *Andira legalis* occur within a few meters distance from each other. However, in previous studies we found marked differences between sun and shade plants. For instance, sun plants are short (1.5 m of height) and invest highly in wide underground organs from where numerous ramets emerge, whereas shade plants are taller (up to 5.0 m tall), not so conspicuous and clonal growth is not apparent (Cirne & Scarano 2001). Sun plants have negative spatial association with other local shrubs and herbs, suggesting a competitive effect, whereas no such pattern is found for the shade plants (Cirne *et al*. 2003). Finally, sun plants nodulate and fixate nitrogen, unlike shade plants (Scarano *et al*. 2001; Geβler *et al*. 2005).

In this study, we examined to which extent this large architectural, physiological and ecological variation between neighbouring plants under contrasting light regimes is matched by variation in leaf anatomy and morphology. It is well known that most plant species have the ability to develop distinct leaves when growing under distinct light levels (Ashton & Berlyn 1992; Chazdon & Kaufmann 1993; Lee *et al*. 2000; Núñez-Oliveira *et al*. 1996; Strauss-Benedetti & Berlyn 1994), and wide variation has been described to several species of the Brazilian Atlantic forest complex subjected to sun-shade extremes (Scarano *et al*. 1999; 2002; Rôças *et al*. 2001; Mantuano *et al*. 2006). However, most such studies were either set in the laboratory or in the field covering broad geographic ranges. Here leaf variation in anatomy and morphology for *Andira legalis* is examined for plants in two adjacent habitats (sun *vs*. shade),

however within only a few meters of distance from each other.

Materials and methods

Study site and studied species – Samples were collected in the Jacarepiá State Ecological Reserve, in the municipality of Saquarema, on the northern coast of Rio de Janeiro state, southeastern Brazil (22º47'-22º57'S and 42º20'- 42º43'W). Mean annual rainfall is 1000 mm and mean annual temperature ranges from 24 to 26 ºC. The swale between forest and strand line is covered by marsh vegetation dominated by Graminae and Cyperaceae, except where a spit of sandy soil, some 200 m long by 70 m wide (maximum) extends from the forest edge almost to the beach. The spit vegetation shows a striking dominance of the legume shrub *Andira legalis* (Vell.) Toledo and the geophyte palm *Allagoptera arenaria* (Gomes) O. Kuntz. There is no transitional zone between the forest, where *A. legalis* is less abundant, and the open shrubland. Thus, *Andira* plants from forest or shrubland, which are closest to the border between the two habitats, are ca. 20-30 m far from each other. Nevertheless, light regime changes abruptly from one formation to the other. Measurements of photosynthetic active radiation (PAR) for both sites (5-50 μE m^{-2}s^{-1} for the dry forest and 1500-2000 μE m^{-2}s^{-1} for the spit) showed clearly the light distinctions between them (Cirne & Scarano 2001; Scarano *et al*. 2001; 2002; Cirne *et al*. 2003).

The genus *Andira* A.L. Jussieu has 29 Neotropical species, with two subspecies occurring in Africa (Pennington & Gemeinholzer 2000). *Andira legalis* is a legume shrub restricted to the coastal vegetation from southeast to northeast Brazil (Mattos 1979), occurring in both exposed (open shrubby vegetation in the sandy coastal plain) and shaded environments (in coastal or low montane forest). Contrasting with the majority of the species in the genus, it has big fruits that are probably dispersed by large rodents (Pennington & Gemeinholzer 2000). Although some fruit production has taken place, seedlings have not been found since 1996, suggesting that much asexual reproduction takes place for this species in the area. For this species, this seems to be true of other localities along the Rio de Janeiro coastline (e.g., Zamith & Scarano 2004).

Sampling, measurements and statistical analysis – For the anatomical analysis five leaves were collected from each of five adult individuals randomly chosen in the sun-exposed and the shaded habitat, at total of 50 samples. Fully expanded leaves, collected from the upper node, were immediately fixed in the field in formaic-acetic acid-alcohol (FAA) (Berlyn & Mishke 1976).

Tissues were gradually dehydrated in ethanol and embedded in glycol methacrylate resin (Johansen 1940). Then, 6 mm transverse sections were made using a rotary microtome, and were subsequently stained with 0.1% toluidine blue and safranin (Feder & O'Brien 1968). The following leaf anatomical parameters were measured: total leaf thickness, mesophyll thickness (spongy and palisade tissue), thickness of the outer periclinal cell wall, thickness of the adaxial and abaxial epidermis and vascular bundle transversal section area, and common epidermal cells, stomata and trichome density. In order to find out as to whether changes in number of stomata between sites were related to cell size reduction, we measured the proportion stomata:total epidermal cells. Tissue layers were quantified by using an Olympus BH2 microscope with the aid of an ocular micrometer. The proportion of sclerenchymatic area of the midrib was calculated using the image analysis program Image-Pro Plus. The video image was acquired by using a Sony video camera attached to the same optical microscope. Stomata, common epidermal cells and trichome density (number per mm^2) were measured in a light microscope, after epidermal dissociation using Jeffrey's reagent (Jensen 1962). In order to express the variation inside and between leaves in the two populations analyzed, for each parameter described above one measurement were performed in slides of the 25 leaves collected. As a result, n = 25 for each of the parameters analysed in each population. Histochemical tests were made to identify tannins (phloroglucinol test) and calcium oxalate (chlorohydric acid) (Johansen 1940).

For morphology, quantitative data were obtained from five leaf samples collected at random from 20 individuals of each site. Leaves were placed on ice in the field and subsequently measured for saturated weight to assess leaf succulence (LS= (maximum fresh weight-dry weight)/area) (Mantovani 1999). Dry weight was measured after oven drying leaves for 72 h at 80 ºC. Leaf specific mass (LSM) was calculated as the ratio between blade leaf area and dry weight (Witkowski & Lamont 1991). Later, anatomical and morphological parameters were compared statistically between sites using the Student's t-test (p = 0.05) (Zar 1996).

Results

In all leaves, the epidermises were single-layered in both faces. A wider variation has been observed for the adaxial than for the abaxial epidermis, including the outer periclinal cell wall. Outer periclinal cell wall nearly doubled across light extremes (Fig. 1 and 2A-B). The epidermal cells of sun-exposed leaves were thicker than those of the shaded. The outer periclinal cell walls of sun-exposed
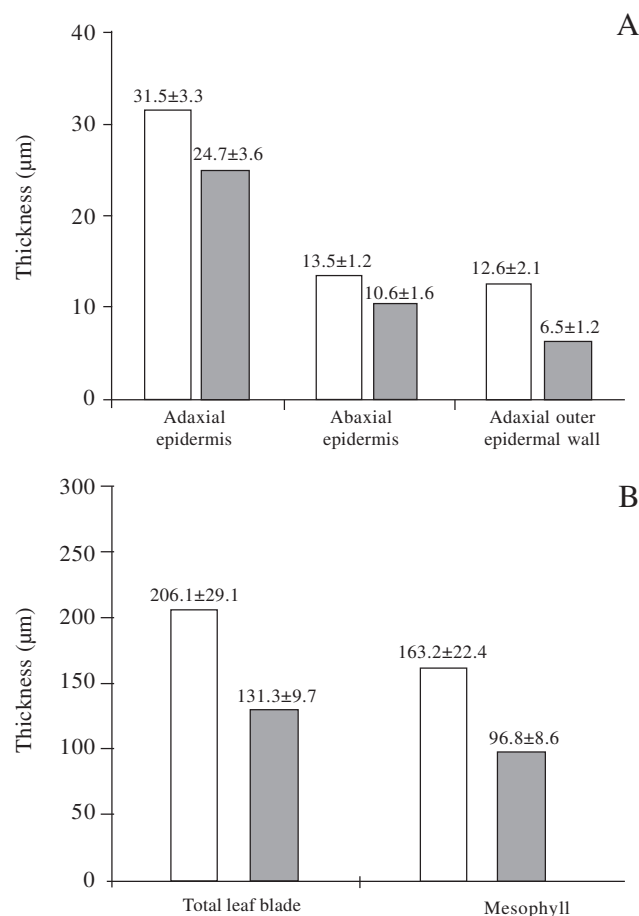

Figure 1. Leaf anatomy traits of sun-exposed (dotted bars) and shaded plants (striped bars) of *Andira legalis* (Vell.) Toledo (n = 25, for each sub-population). A. Thickness of the adaxial epidermis, abaxial epidermis and adaxial outer epidermal wall. B. Total leaf blade and mesophyll thickness. Top values are mean ± standard deviation. All values were significantly higher for the exposed plant (Student's t-test; p<0.01).

plants were concave whereas in shaded plants they were relatively flat (Fig. 2A-B). Moreover, epidermal cells of sun-exposed leaves showed an apparently higher tannin content than shade leaves (Fig. 2A-B). All leaves exhibited paracytic and anisocytic stomata only at the abaxial surface, characterizing hypostomatic leaves. The frequency of stomata per unit area was significantly higher in sun-exposed than in shade leaves. However, there was no difference between them for the proportion stomatal: total epidermal cells (Tab. 1). Still, at the abaxial face there were multicellular trichomes composed by a row of 3-8 cells, with the distal cell being longer than the others (Fig. 2C-D). Trichome density did not show significant differences between the two sites (Tab. 1).

In addition to the expected quantitative differences between sun-exposed and shaded leaves, *A. legalis* showed striking qualitative differences in the leaf anatomy. Shade plants had a dorsiventral mesophyll, with
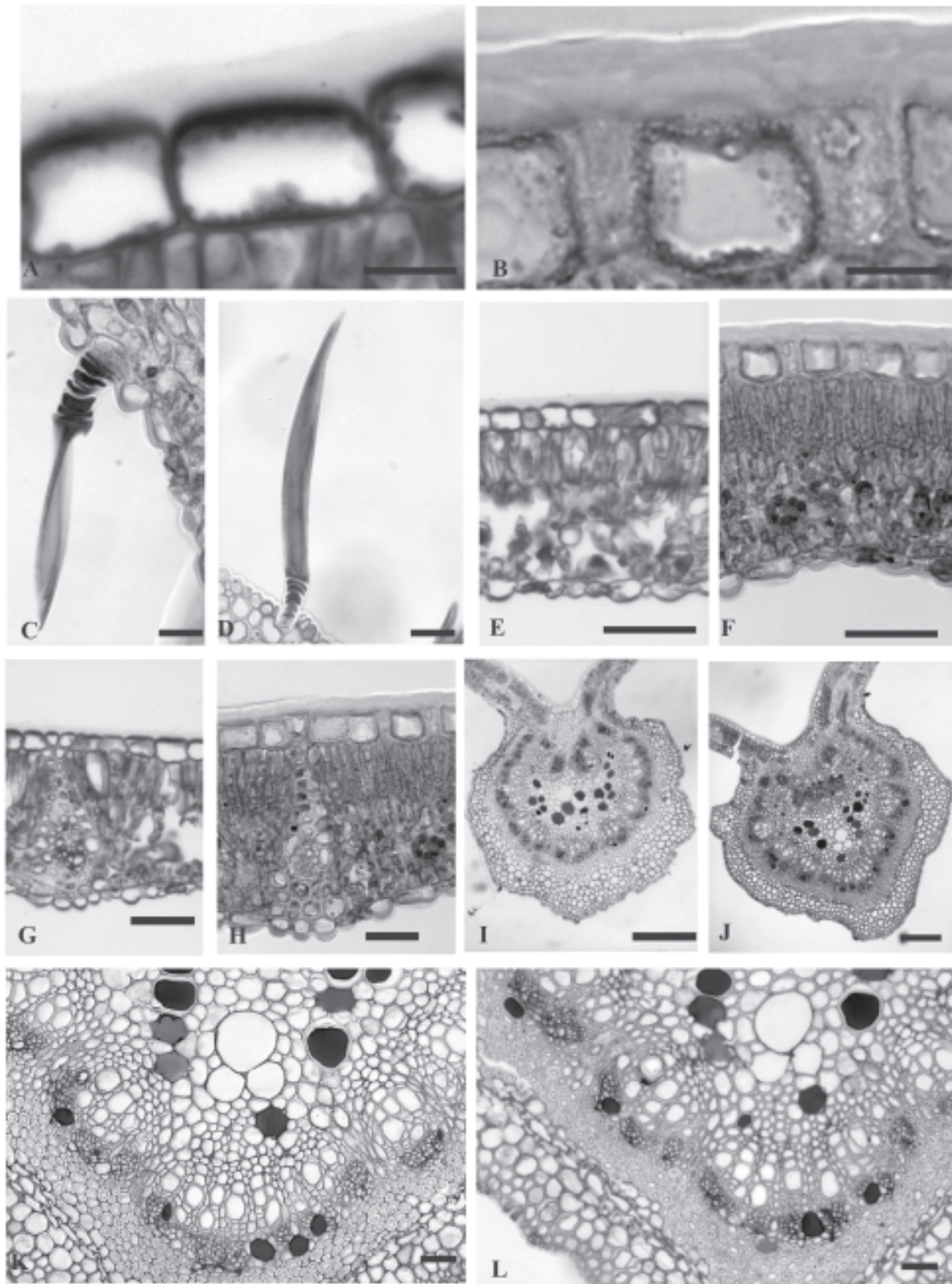
Figure 2A-L. Transverse section of the leaf of *Andira legalis* (Vell.) Toledo. Adaxial epidermis: A. Shaded. B. Sun-exposed. Trichome: C. Shaded. D. Sun-exposed. Leaf blade: E. Shaded. F. Sun-exposed. Collateral bundle of a vein: G. Shaded. H. Sun-exposed. Midrib: I, K. Shaded. J, L. Sun-exposed. Bars: A-B = 25 μm; C-D = 20 μm; E-H, K-L = 50 μm; I-J = 100 μm.

palisade parenchyma with 1 or 2 cells layers and a spongy parenchyma with 2 or 3 layers (Fig. 2E). On the other hand, the sun-exposed plants exhibited a unilateral mesophyll (Fig. 2F). Moreover, the leaves of sun-exposed individuals showed higher total leaf thickness and mesophyll thickness (Fig. 1B). Changes in mesophyll thickness were apparently caused by cellular elongation and differentiation of multiple palisade layers in response to increased light. Mean leaf extension was significantly higher ($p < 0.05$) in the forest (55.9 cm) than in the open area (48.6 cm).

For both sites the veins showed collateral bundles surrounded by sclerenchymatic fibres (Fig. 2G-H). Apparently, sun-exposed leaves had a higher density of veins, which could be related to the smaller leaf area in this habitat. Sheath cells were observed with extensions for both faces. In these cells, under the abaxial face, calcium oxalate crystals were identified as well as phenolic substances as tannins (Fig. 2G-H). However, the proportion of these compounds in each habitat was not measured.

A transverse section of the midrib showed an arc of collateral bundles surrounded by fibres and a sclerified parenchyma in both environments (Fig. 2I-L), however the midrib total area was significantly higher in the sun-exposed leaves (Fig. 2I-J; Tab. 1). These anatomical results correlated with the leaf morphological characters measured (leaf specific mass and leaf succulence), which similarly had higher values in the sun-exposed plants.

Discussion

The clear differences in population structure, plant morphology and physiology between two sub-populations of *A. legalis* in this restinga ecotone (Cirne & Scarano 2001; Scarano *et al*. 2001; Cirne *et al*. 2003; Geβler *et al*. 2005) are matched by a marked variation in leaf structure. The anatomical structure found in the sun-exposed plants suggests a strong tendency to xeromorphism when compared with shade plants (see Esau 1977). The direct relationship between thickness and radiation is consistent with several other studies (Strauss-Debenedetti & Berlyn 1994; Rôças *et al*. 1997; Lee *et al*. 2000). The palisade tissue in sun-exposed leaves of *A. legalis* was also wider than in shade plants, which eases light penetration under direct light incidence (Vogelmann & Martin 1993) and increases photosynthetic potential (Ashton & Berlyn 1994; Chazdon & Kaufmann 1993; Esau 1977; Strauss-Debenedetti & Berlyn 1994) due to more photosynthesising cells per unit leaf area. This great structural difference between plants in adjacent localities is striking and may indicate a wide ecological plasticity of this species (see Bazzaz 1996).

The high variation observed in the outer periclinal cell wall was responsible for most of the difference found in the adaxial epidermis between the two habitats. A thicker cuticle, such as that often seen in plants of sun-exposed areas (Ashton & Berlyn 1994), must provide a permanent biological resistance against water loss, generating low leaf water potentials protecting against desiccation during dry and windy spells (Fahn 1985; Schreiber & Riederer 1996). The different shape of the outer periclinal cell wall between sun and shade leaves affects light distribution inside the leaf. Common epidermal cells converge diffuse light to the chlorophyllian tissue of shade leaves, and alternatively reduce direct light inside of sun-exposed leaves through reflectance reducing the risks of potential damage (Lee *et al*. 1990). The apparently higher tannin contents in the epidermal cells of sun-exposed leaves may act as another barrier against light penetration in these plants.

The proportion of stomatal:total epidermal cells was similar for both sites, because the higher stomatal density in sun-exposed plants was probably related to the smaller leaf size and consequently the smaller cell size when compared with shaded plants that had larger leaves. The lack of significant difference between sun-exposed and shade plants regarding leaf trichome density suggests that this trait is not related to plant acclimation to light in this species.

Table 1. Leaf anatomy and morphology parameters of *Andira legalis* (Vell.) Toledo (mean ± standard deviation) of sun-exposed and shaded plants (n = 25, for each sub-population). MA - midrib area; SD - stomata density; S:TEC - proportion stomatal:total epidermal cells; TD - trichome density; LSM - leaf specific mass; LS - leaf succulence. *indicate significant differences at $p < 0.01$ (Student's t-test); NS - non-significant.

	Sun	Shade	t	df	F
MA (mm^2)	1181.4 ± 142.8	522.7 ± 112.6	8.1	8	1.6*
SD	549.0 ± 62.8	374.5 ± 33.9	5.5	8	3.4*
S:TEC	14.4 ± 2.2	13.6 ± 1.5	0.02	8	0.02 [NS]
TD	21.4 ± 5.4	18.6 ± 5.3	0.8	8	1.07 [NS]
LSM (g m^{-2})	169.9 ± 12.3	70.7 ± 3.3	32.1	38	13.8*
LS (g m^{-2})	174.3 ± 19.6	112.7 ± 15.8	10.1	38	1.5*

High values observed for leaf specific mass (LSM) are often associated with concentration of structural material and formation of protective tissue for desiccation and herbivory (Choong *et al*. 1992; Medina *et al*. 1990; Turner 1994). According to Witkowski & Lamont (1991), LSM has two components responsible for these variations: leaf density and thickness. Density is expressed by thickness of the cuticle and cell walls, extension and abundance of air spaces, and vascular bundles. In contrast, leaf thickness varies mainly with leaf shape, number of layers and length of palisade cells. Both factors may vary independently and therefore may be controlled by different environmental parameters (Niinemets *et al*. 1999). In *A. legalis*, the higher increase in the dry mass (140%) than in thickness (57%) in the sun-exposed leaves may suggest that leaf density could be the main factor leading to high LSM values, as found by Garnier & Laurent (1994) for temperate grasses. In fact, this is confirmed by the very high amount of sclerenchymatic tissue of the midrib and the more densely packed mesophyll cells observed in sun-exposed leaves of *A. legalis*.

The increase of leaf succulence (LS) in sun-exposed plants may be related to a higher leaf thickness. Although these plants did not have a typical water parenchyma, the higher leaf volume occupied by the protoplasm of the epidermal cells and mesophyll could be responsible for the higher water storage in this organ (Garnier & Laurent 1994; Kluge & Ting 1978).

These results showed a high degree of variation in regard to leaf anatomy for this tree species within an ecotone, in a very small geographic area. This is in harmony with previous results regarding variation in growth, morphology and physiology for this species. The fact that in the study area the species shows a considerable contribution of asexual reproduction to plant recruitment (Cirne & Scarano 2001) suggests that such ecological variation may take place even in a population with a possibly small genetic variability. This potential to adjust to distinct environments may explain in part the ability of this and many other Atlantic forest species to have successfully migrated in the past from a mesic forest environment to a dry, open environment such as the restingas (see Rizzini 1979; Scarano 2002). Scarano *et al*. (2001) investigated the ecophysiological behaviour of many Atlantic forest and restinga species and concluded that adaptation to the high light levels in the restinga habitats does not seem to have been fully achieved yet, as indicated by the commonness of chronic photoinhibition and lower energy dissipation capacity. *Andira legalis*, however, showed a better photosynthetic performance in exposed sites than many other woody species of the restinga (see also Geβler *et al*. 2005).

This could possibly be related to the efficient anatomic apparatus here described.

Acknowledgements

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